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Natural and anthropogenic drivers of Bornean elephant movement strategies

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ABSTRACT

Endangered Bornean elephants are severely threatened by ongoing habitat transformation and increasing levels of human-elephant conflict. Understanding how elephants move across intact and transformed landscapes, as well as within them, is therefore of vital importance for the successful implementation of conservation management initiatives. We combined remote sensing and GPS telemetry data to identify broad habitat utilization and key movement areas to aid elephant management and conflict mitigation in three spatially-isolated populations in central and eastern Sabah, Malaysian Borneo. Home ranges were estimated using Brownian Bridge Movement Models and specific behavioral movement traits were identified by pathway analyses. These behavioral traits enabled a fine-scale evaluation of movements between and adjacent to forest patches and the role of large-scale agriculture in shaping elephant movements. Both natural (topological) and anthropogenic (agricultural) landscape features were found to have a broad influence on elephant movements. All elephant populations exhibited human-mediated behavioral responses, regardless of disturbance level. Throughout their range, elephants appeared to actively select relatively degraded forests, as measured by aboveground carbon density. However, elephants actively avoided urbanized areas, including roads and villages. Throughout the elephant range, high-speed, low-trajectory movements were found at low aboveground carbon locations, with 27% of all such movements located in large-scale agriculture. Our results suggest that agriculture impacts movement strategies of elephants, with evidence of repeat agricultural use pointing towards an active rationale for this behavior. Elephants were also found to use ridgelines as movement pathways, providing further context for the protection of such forested areas. The Lower Kinabatangan population, located in small remnant forests, travelled further to meet their ecological needs, suggesting the population is under added strain. Our work represents the broadest landscape assessment of Bornean elephant movements to-date and has important implications for both future work and habitat-level protected area management strategies.

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1. Introduction

Remote sensing observations have had a major influence on conservation planning by providing new insights into how both plants and animals utilize landscapes at fine spatial and temporal scales (Davies and Asner, 2014; Gould, 2000; Nagendra et al., 2013; Pettorelli et al., 2014; Turner et al., 2003). Likewise, remote sensing has aided in the demarcation and protection of wildlife corridors, with connectivity between habitat crucial to the survival of all but the most adaptable of species (Mallegowda et al., 2015; Viña et al., 2010; Wei et al., 2015). Identification of corridors has been the subject of much research, with numerous strategies developed to predict animal movement (Boyce and McDonald, 1999; Epps et al., 2007; McRae et al., 2008; Thurfjell et al., 2014). The use of airborne Light Detection and Ranging (LiDAR) has expanded rapidly over the last decade, with many efforts to assess wildlife movement and habitat selection as they relate to vegetation structure and terrain. Studies have examined habitat use by a range of mammals (Ewald et al., 2014; Loarie et al., 2013), birds (Clawges et al., 2008; Goetz et al., 2010; Olah et al., 2017), and insects (Davies et al., 2014; Vierling et al., 2011). Pairing of such high-resolution habitat data with animal movement data provides added validation to movement-based models and improved understanding of animal habitat selection. One pertinent application of such data coupling is the assessment of corridor use by wildlife (Bastille-Rousseau et al. 2018; LaPoint et al., 2013; Whittington et al., 2005) and the identification of "animal-defined corridors" (see LaPoint et al., 2013). Identification of animal defined corridors have been suggested as a more data grounded and accurate approach for the creation of new corridors, with behaviors such as the frequency of highly directional, rapid movements providing evidence of corridor-like behaviors (Graves et al., 2007; LaPoint et al., 2013).

Elephantidae are often viewed as pillars of conservation across the range of habitats they occur. Indeed, elephants have been shown to provide a net economic benefit to nations with wild populations (Bandara and Tisdell, 2004; Martín-López et al., 2008), partly because they are iconic species and an important component for the ecotourism industry. Asian elephants (*Elephas maximus*) have historically received less conservation attention than those inhabiting more tourist-friendly savanna habitats. Conversely, the difficulties in observing forest elephants have likely shielded them from the highest levels of ivory poaching experienced by savanna elephants (*L. africana*) over the course of more than a century (Douglas-Hamilton, 2009). However, this is beginning to change, with ivory poaching becoming more prevalent for forest elephant populations (Maisels et al., 2013). Bornean elephants (*E. maximus borneensis*) are an endangered sub-species of the Asian elephant, with current estimates suggesting their total population size is below 2000 individuals (Goossens et al., 2016). Bornean elephants have been shown to thrive in degraded landscapes (Evans et al., 2018), however, complete conversion of forests to agriculture has vastly elevated levels of human-elephant conflict (Crespo Mingueza, 2018). This has led to increased levels of poaching, which resulted in at least 25 elephant deaths during 2018 (B. Goossens, pers. comm.), representing at least a 1% die-off of individuals within this 12-month period. Compared to historical figures of 111 elephant deaths since 2010, this represents a vast increase in mortality (B. Goossens, unpublished data). Mitigation of agricultural conflict is a key tool in reducing these preventable deaths (Wadey et al., 2018).

An understanding of home range requirements is an important first step for calculating protected area requirements for animal populations, particularly those engaging in crop raids. For example, understanding home range requirements could enable the protection and incorporation of important feeding grounds, which could in turn reduce crop raids (Shaffer et al., 2018). Alfred et al. (2012) reported Bornean elephant home range size as 250–400 km^2 in non-fragmented forests, and ~600 km^2 in disturbed, fragmented landscapes, providing the first indication that forest connectivity and quality was an important factor in landscape utilization by these mega-herbivores. Forest quality limitations become important when applied to degraded habitats. For example, the Lower Kinabatangan Wildlife Sanctuary (LKWS) elephant population numbers ~250 individuals, but the available habitat is far less than the home range requirements of a single elephant in low-quality habitat (Estes et al., 2012). Examination of how Bornean elephants utilize such degraded landscapes suggested, that range-wide, elephants preferentially seek out forests with shorter canopy (Evans et al., 2018), habitats consistent with degraded landscapes. A complementary study also found that elephants are willing to utilize recovering habitat (Evans et al., 2017), which has importance in terms of creating additional elephant habitat in areas where conflict is most prevalent.

Here, we sought to further examine landscape-level requirements of Bornean elephants by investigating existing population-based habitat adaptations. We aimed to identify population level differences in behavior such as home ranging, as well as to examine finer-scale movement nuances using step selection function. On a population level, we aimed to examine home ranging and the role of agriculture in movement-based behavior. By calculating home range sizes using updated techniques, we further sought to develop more realistic estimates of habitat requirements, and to assess the differences in landscape utilization exhibited by populations with varying levels of range restriction. In order to examine finer-scale movements, we aimed to assess the presence and implications of animal defined corridors (ADC). Finally, we aimed to identify ADC use and the factors most important for their demarcation, which could also serve to identify areas of potential conflict and aid conservation planning efforts.

2. Materials and methods

2.1. Study region

Our study was conducted in the Malaysian state of Sabah, located in northeast Borneo, and focused on forested and forest edge areas of central Sabah (CS) (~1.25 million ha), the Lower Kinabatangan Wildlife Sanctuary (LKWS) (~26k ha), and Tabin Wildlife Reserve (TWR) (~122k ha). These areas encompass the vast majority of the Bornean elephant's range, but are geographically isolated from each other by large expanses of oil palm. The forests included within CS consist largely of contiguous forests interspersed with incidences of other land uses, including large scale agriculture, as well as lower impact management regimes such as mosaic planting and commercial tree plantations. These areas consist of a variety of protection statuses, although the majority of forests within CS consist of either Class I (totally protected) or Class II (commercial) forest reserves. Bornean elephants in Sabah are found throughout the CS region, with other large populations within the LKWS and TWR. These were determined to be distinct populations owing to large areas of agricultural and urban separation. Whilst we cannot definitively rule out individual movement between populations, large-scale GPS tagging efforts suggest that these represent isolated populations (Evans et al., 2018). These three populations account for more than 90% of Bornean elephant individuals globally. Smaller, isolated sub-populations within Sabah were excluded from the analysis due to a lack of GPS collar data.

2.2. GPS telemetry

Twenty-nine adult Bornean elephants were fitted with GPS collars between 2010 and 2017, these included 13 males and 16 females. Satellite collars were obtained from Africa Wildlife Tracking (AWT, Pretoria, South Africa). Collars weighed a total of 14 kg each, less than 1% of the total body weight of an adult elephant (Alfred et al., 2012). All individuals were wild-caught, with some individuals ($n = 15$) darted in oil palm plantations and relocated to the nearest protected forests (<10 km) as part of conflict mitigation efforts. In all cases elephants were moved to familiar forests often just 1–2 km from the capture site and within their home range. The first 14 days of post-collaring data were discarded for each individual owing to potential differences in post-release movement behaviors, as well as to allow for translocated individuals to adapt to their new surroundings (Evans et al., 2018). Movement rates during the first few days following release can also be strongly influenced by effects of anesthesia and stress caused during the collaring process. All units were set to record 12 equally-spaced GPS locations per day, i.e. a location every 2 h.

2.3. Environmental variables

Sabah was aerially mapped in April 2016 by the Global Airborne Observatory (GAO; formerly the Carnegie Airborne Observatory; Asner et al., 2012). Light detection and ranging data from these flights were processed as described in Asner et al. (2018), Evans et al. (2017) and Evans et al. (2018) and upscaled using satellite data following Asner et al. (2018) to ensure full coverage across the Bornean elephant range. Habitat and landscape variables hypothesized to influence elephant movement (following Evans et al., 2018) were used in the analysis. These included top of canopy height (TCH), aboveground carbon density, using the data layer derived by Asner et al. (2018), as well as slope, relative elevation above the nearest drainage line (with drainage lines equal to 0 and hillcrests equal to 1), and vector ruggedness measure (VRM) (Sappington et al., 2007). All data layers used had a spatial resolution of 30 m.

2.4. Analysis

Population-based elephant densities were calculated from estimates of forest cover for each of the three regions (population estimates over available forest habitat for the LKWS, TWR, and CS populations), as well as estimated population figures for each of these populations. An ANOVA was performed to assess if there were differences in home range between relocated and non-relocated individuals. Population estimates were based on figures from Alfred et al. (2011) and Estes et al. (2012), although these figures were updated (B. Goossens & Sabah Wildlife Department, pers. comm). Estimates of elephant home ranges were established using dynamic Brownian Bridge Movement Models (dBBMMs) (Kranstauber et al., 2012). Home range models were fitted for each individual across Sabah, with both core (50%) and total (95%) home range models calculated. Modelled movements of individuals were assessed using the R package *move* package (v2.1.0). Movements were stacked to combine populations and were assessed for high-speed, low-trajectory movement (HSLT) changes. Movement between points was determined to qualify as high-speed if it fell within the upper quartile of movement rates within an individual's dataset. Conversely, low-trajectory changes were determined by isolating those trajectories that fell in the lower quartile of trajectory changes within the dataset. These criteria were combined to produce high speed, low trajectory locations (following Kranstauber and Smolla, 2013). Locations were further examined to isolate where HSLT locations occurred on at least three temporally distinct occasions. Movements of each individual were assessed for movements meeting these HSLT prerequisites. High-speed, low-trajectory movements with minimum repeat ($n = 3$) usage and within close proximity (<1 km) to each other were deemed to represent ADCs.

To understand drivers of elephant movement within each HSLT ADC, we created buffers 100 m either side of these ADCs to encapsulate potential GPS error and to provide an area within which the habitat could feasibly be expected to influence individual movement decisions. Points within these buffers were assessed for strings of temporally connected points, and movements with at least eight consecutive fix locations deemed to constitute a movement string that was utilized for further analysis. Movement strings were temporally independent from one another, and each string consisted of points from a single individual. Step-selection functions (SSF) of elephant movement within each string were then developed using Geospatial Modelling Environment (GME) software (Beyer, 2012). Each actual movement step was compared with 10 randomly selected available steps using a Cox mixed logistic regression to examine the habitat and terrain variables that most influence the movement of elephants through the ADCs. Maximum random step length was given as the maximum known step length from within an individual's dataset. The Cox mixed logistic regression allowed the SSFs to be analyzed independently of variation attributed to an individual's movement. Models were assessed using Akaike's Information Criterion corrected for small sample sizes (AICc) with the initial global model dredged using the R package *MuMIn* (v.1.40.4). Model selection was performed on the top weighted models, with model averaging performed to take each of these top models into account.

Environmental variables for ADCs were then compared to the entire Bornean elephant range, and GPS location means to assess if the HSLT ADCs deviated significantly from available elephant habitat across Sabah. Species distribution model layers created by Evans et al. (2018) were used to provide indications of habitat suitability within the ADCs. In addition, 1 km buffers were created surrounding urbanized areas, including villages, towns, and roads, to assess whether direct anthropogenic disturbance influenced elephant presence in these areas. This was achieved by comparing GPS location rates within the 1 km urban buffer zones to incidence rates throughout the study area. These analyses were conducted using QGIS (v. 2.18.7).

3. Results

Twenty-nine adult elephants were collared for a mean of 450.2 (±307.4) collaring days. The overall mean home range of individual elephants (95% utilization) was 149.27 (±108.70) km^2, with a mean core home range (50% utilization) of 11.60 (±12.91) km^2. Whilst females had generally larger ranges, there was no significant difference between home range sizes of males (86.47 (±52.51) km^2) and females (183.53 (±117.77) km^2) ($p = 0.07$) (Fig. 1). There was no significant difference between the home ranges of relocated individuals and those collared in forest ($p = 0.97$). Mean aboveground carbon density (ACD) at known GPS locations was 58.11 (±47.36) Mg C ha^{-1}, which is consistent with ACD values in degraded forests; unlogged forests average over 200 Mg C ha^{-1} in Sabah (Asner et al., 2018).

There was no significant difference in total home range size when the three populations (LKWS, TWR and CS) were compared ($p = 0.27$). However, when examined in isolation, the LKWS population exhibited significantly larger home ranges than the CS population ($p = 0.026$) (Fig. 2a). There was also a significant difference in core home range sizes between the populations ($p = 0.038$), with LKWS ranges being larger than both the TWR and CS populations.

Population density within each of the three isolated populations varied greatly, with densities of elephants in LKWS being almost eight times greater than that of the other populations (LKWS = 0.625 individuals per km^2; CS = 0.08 individuals per km^2; TWR = 0.082 individuals per km^2). There was also a disparity in frequencies of HSLT movements per unit area across the populations. Incidences of HSLT movement, per km^2 of forest available, across the three populations totaling 5.75 km^2 for the LKWS, 0.01 km^2 for CS, and <0.01 km^2 for TWR. When HSLT points were examined as a percentage of the total dataset, the intra-population values were roughly equivalent for both the LKWS (0.26%) and CS (0.23%) populations. However, the TWR population exhibited vastly reduced rates of HSLT movements, with just 0.03% of locations meeting these criteria.

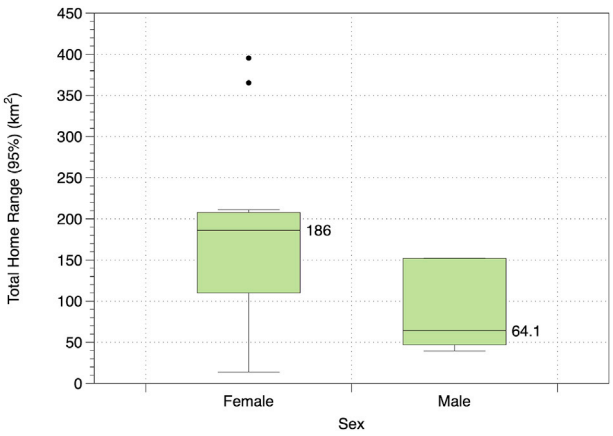

Fig. 1. Boxplots depicting total (95% utilization) elephant home range sizes, separated by sex (13 males and 16 females). Home range was assessed using dynamic Brownian Bridge Movement Model (dBBMM) analysis.

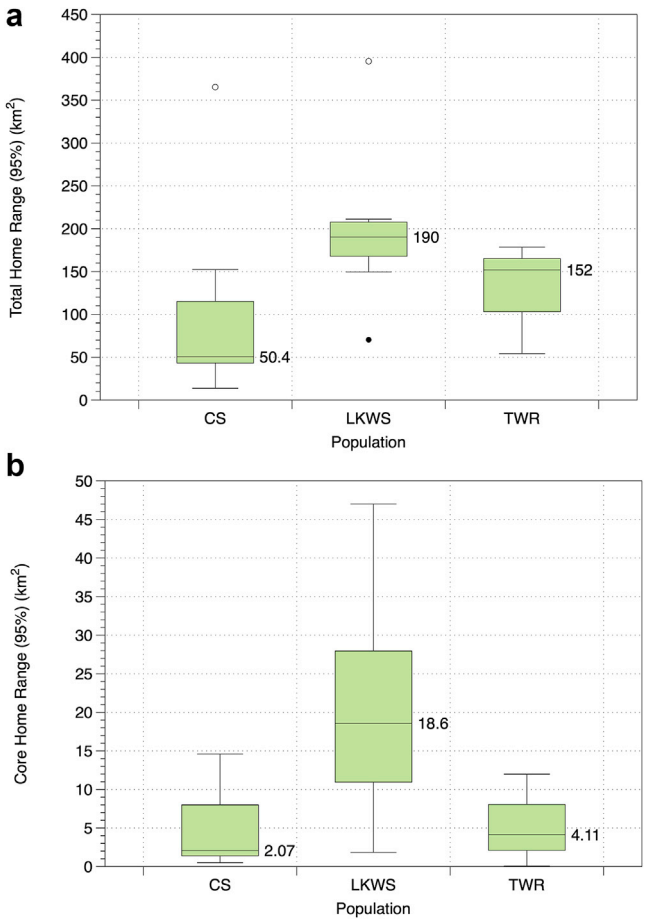

Fig. 2. Boxplots depicting home range sizes for the three spatially isolated Bornean elephant populations (CS, n = 12; LKWS, n = 12; TWR, n = 5): 2a: total home ranges 95% utilization and 2b: core home ranges (50% utilization). Home ranges were assessed using dynamic Brownian Bridge Movement Model (dBBMM) analysis.

HSLT points represented just 0.23% of the total number of elephant GPS points in the entire dataset, with 27% of them occurring within lands converted for agriculture: 24.2% in oil palm plantations, 0.7% in timber plantations, 0.58% in oil palm mix, and another 0.05% in rubber plantations. In contrast, throughout the elephant collaring period, only 2.7% of all GPS locations were recorded within agriculture, resulting in a substantially higher proportion of HSLT movements in non-forest or forest-mix habitats than would be expected if these movements were evenly distributed across all landscape classes. HSLT points across the range had a mean TCH of 11.44 (±6.52) m and a mean ACD of 44.64 (±22.55) Mg C ha^{-1}, which was 24% lower than the mean ACD across all known locations. When assessed for mean habitat suitability, as defined by Evans et al. (2018), HSLT movements exhibited a mean suitability of 0.459 (±0.116), suggesting that HSLT movements were recorded in slightly sub-optimal habitat conditions (optimal suitability ranged from 0.484 to 0.977). This figure is lower than the suitability of all known elephant GPS locations throughout the range (0.56). However, these figures are considerably higher than those of the range-wide mean (Table 1).

Increasingly, how elephants interact with human settlements, and the danger posed to them by roads is a major facet of elephant conservation. However, of the more than 160,000 discrete GPS locations recorded, just 1.54% of them occurred in the vicinity (1 km) of urbanized areas (roads, villages, and towns). This is despite these areas representing 14.85% of the occupied by the three populations. Furthermore, a mere 0.26% of HSLT movements occurred in the vicinity of human disturbance.

The spatially compressed LKWS population, existing in thin, riparian areas and bordered by large, contiguous oil palm plantations, appeared to have to travel further, based on increased total and core home ranges sizes, to meet ecological needs than individuals present in forest blocks (Estes et al., 2012). The restricted nature of their riparian habitat resulted in HSLT movement criteria being more commonly met (Fig. 3). The increased frequency of HSLT movements meant that it was impossible to accurately delineate HSLT ADCs for this population. As such, the LKWS population was removed from subsequent corridor delineations. HSLT points from the two remaining populations (TWR and CS) resulted in the identification of 42 HSLT ADCs throughout the study area (Fig. 4). These ADCs were delineated using movement data strings from 14 individuals: 10 males and four females, which provided enough contiguous data points to perform SSF analysis.

Table 1
Variation in habitat variables within delineated animal-defined corridors (ADCs) and throughout the GPS-derived total elephant range, across all individuals, as well as the non-GPS derived range-wide mean. Vector ruggedness measure (VRM) was calculated following Sappington et al. (2007). Slope measurements were assessed based on elevational maps of Sabah. Tree canopy height (TCH) was derived from 30 m resolution upscaled LiDAR data. Habitat suitability index is from Evans et al. (2018).

	ADC (mean)	StDev	GPS location (mean)	StDev	Range extent (mean)	StDev
Elevation (m)	183.78	118.87	97.64	128.4	452.37	161.31
Slope	4.74	1.94	3.1	2.63	6.9	3.92
VRM	0.245	0.12	0.39	0.25	0.2	0.2
TCH (m)	14.2	6.21	11.75	7.31	13.76	7
Habitat suitability Index	0.46	0.12	0.56	0.11	0.37	0.11

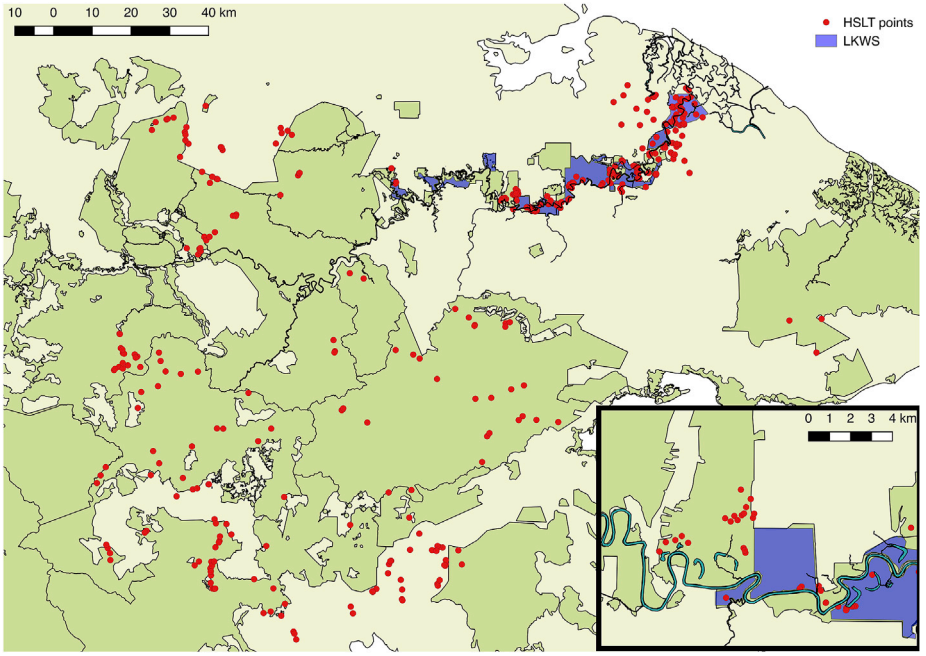

Fig. 3. High-speed, low-trajectory (HSLT) movements from across the Bornean elephant range, with forested areas denoted in green. Higher densities of HSLT movements exist in the LKWS population. This isolated population exhibits almost as many occurrences of these points as the rest of Sabah combined. Inset – High density HSLT movements from the edge of the elephant's range in the LKWS, displaying higher densities of HSLT points. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Presence of ADCs were often aligned with natural barriers such as habitat edges, both natural and anthropogenic (Fig. 5). HSLT points, together with 100 m flanking buffers, were used to demarcate ADCs. Animal-defined corridors had a mean length of 5.50 km (±4.49 km). Overall, ADC locations were found at lower elevations than the range-wide mean, but higher than the mean of all elephant GPS locations (Table 1). Animal-defined corridor behaviors were found to be present in a number of habitat and topological situations, skirting forest edges, through oil palm agriculture, and following natural topological features. Of the 42 ADC locations delineated, 28 closely bordered, or were found within, large-scale agricultural systems.

Temporally-consecutive strings of movement data were available from nine delineated ADCs. These nine ADCs were represented by 15 discrete movement data strings from five individuals (four males and one female). The nine ADCs were evenly distributed throughout the central Sabah population's range and located in forest or forest-edge habitat (Fig. 4).

The nine ADCs selected for SSF analysis were, broadly speaking, representative of habitats encapsulated by the complete network of ADCs identified. SSF ADCs were located alongside agriculture, tracking rivers, and at a range of elevations. Mean elevation of SSF ADCs, at 192 m (±477 m), was highly comparable; all identified ADCs had a mean elevation of 184 m (±979 m).

SSF analysis indicated that relative elevation was the most significant factor driving movement decisions ($p = 0.04$) (Table 2). There was an increase in relative elevation between movement steps, with increased probability of small increases in relative elevation, such as can be the case when following ridgelines. Canopy cover and slope were not significant predictors for step selection. In addition, there was a trend for elephants to select steps with lower TCH, although this was not significant ($p = 0.07$).

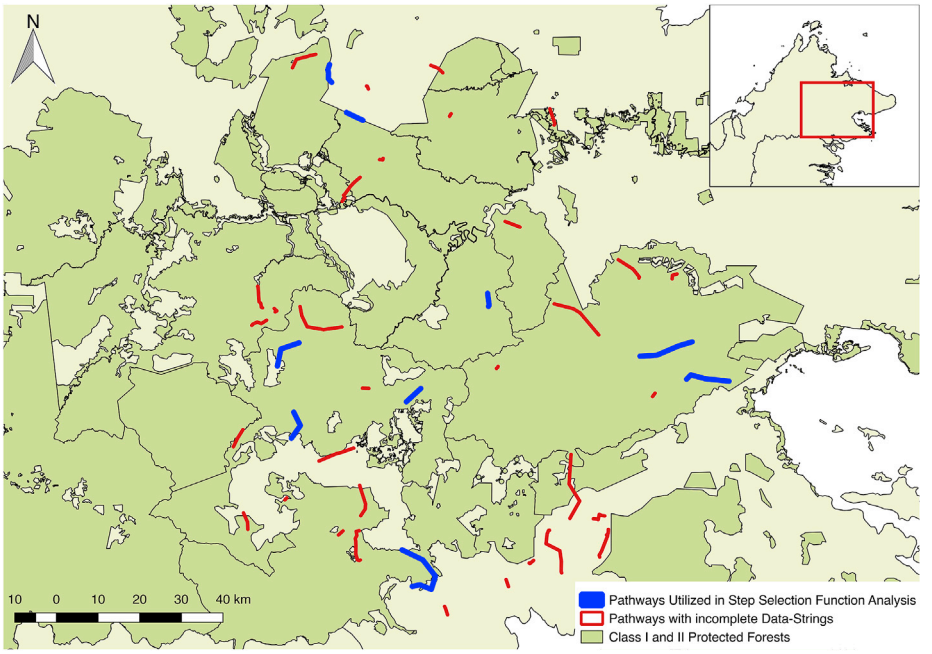

Fig. 4. Geographic distributions of animal defined corridors (ADCs) determined by isolating multiple use, high speed, low trajectory (HSLT) movements. ADCs in blue indicate those for which step selection function (SSF) analyses were performed. Red ADCs were not utilized in SSF analyses as they did not fulfill the minimum requirements in terms of the number of consecutive points. The location of the study region within Sabah, Malaysia is shown in the inset. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

4. Discussion

Little is conclusively known about how Bornean elephants utilize the landscape. Previous work to ascertain home range sizes have been geographically restricted (Alfred et al., 2012). Here, we provide not only baseline information on habitat requirements and utilization by Bornean elephants at a scale not previously attempted, but also show how habitat alterations by humans impact the daily movement and specific behavioral traits of these charismatic megaherbivores. Elephants forced to inhabit isolated, restricted "corridor-like" landscapes, such as the LKWS population, must travel further to fulfill their ecological needs. This translates into increased home range sizes and more direct, rapid travel than populations in less disturbed landscapes, such as the CS population. However, populations exposed to relatively low disturbance, such as the CS population, still exhibit signs of human-mediated behavioral responses throughout their range suggesting a preference and selection of "low-quality" habitat, in terms of ACD, which is consistent with findings from previous studies (Evans et al. 2017, 2018).

The use of ridgelines, the potential for which has been suggested here, adds weight to the anecdotal reports of the importance of these features in elephant ranging, and highlights the that ridgelines have potential for habitat connectivity. Animal-derived corridors were split between natural and anthropogenic habitats, although the proportion of HSLT movements, within each habitat, was disproportionately weighted towards agricultural landscapes. This suggests adaptive behavioral strategies to cope with human conflict, potentially with elephants utilizing plantations as a food source. This suggests that this behavioral response is present as both a natural behavioral mechanism, used when navigating topographic features, and a newly adapted behavioral response to habitat fragmentation (Fig. 5). The preponderance of HSLT ADCs in oil palm plantations could also suggest that such movement behavior does not necessarily indicate the delineation of strict habitat corridors, in the sense of corridors that physically connect otherwise isolated habitat patches. Instead, these HSLT areas in oil palm plantations could indicate zones where elephants move rapidly and with definitive directionality; such movement could be driven by the presence of true corridors, food availability, the presence of electric fences, or as a consequence of the threats posed to elephants in low-quality (i.e. plantation) habitats where human-elephant conflict and resultant stress responses are more likely to occur.

Increasing levels of human-elephant conflict threaten the medium-to long-term existence of the Bornean elephants. Here, we improved home range estimates for Bornean elephants, with home ranges calculated to be, on average, two-thirds smaller than previously reported (Alfred et al., 2010; Alfred et al., 2012). This has wide-reaching implications for the potential carrying capacities of the remaining forests throughout the Bornean elephant range. However, the connectivity of these forests plays a key role in the future survival of each of the different populations, and how they utilize the landscape. In areas where remaining forests retain a corridor function, such as the LKWS population, core home ranges were significantly larger than

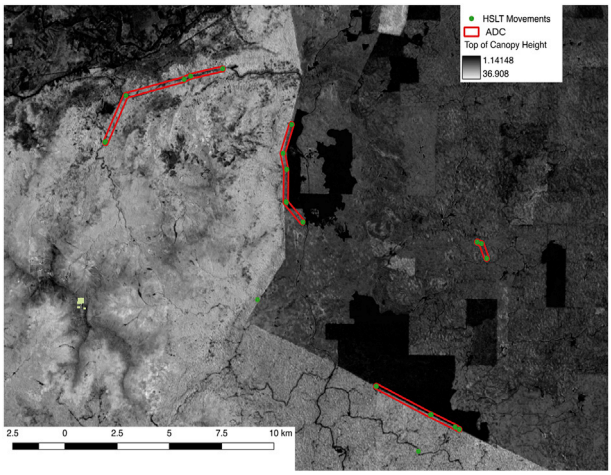

Fig. 5. High speed, low trajectory (HSLT) movements linked by proximity to delineate animal defined corridors (ADCs). In this example, ADCs are found to follow agricultural boundaries, rivers and ridgelines.

Table 2
Cox mixed-logistic regression summary for habitat and terrain variables within elephant ADC buffers.

Habitat Variables	β	StDev	z value	p value
Relative elevation	0.012	1.012	0.006	0.04
Tree canopy height	−0.054	0.947	0.031	0.077
Canopy cover	−0.031	0.969	0.635	0.96
Slope	0.007	1.008	0.03	0.8

either the TWR or CS populations (Fig. 2b), suggesting that individuals needed to travel further to meet basic ecological needs (Alfred et al., 2012).

Across all individuals, elephants were found to select areas of "low" habitat quality, as defined by carbon stocks, with a mean ACD of 58.11 Mg C ha^{-1}, whereas unlogged, intact forests in Sabah average greater than 200 Mg C ha^{-1} (Asner et al., 2018). The importance of degraded landscapes for elephants was suggested by Evans et al. (2018), who stated that only 26% of forests in Sabah were deemed of "high-quality" for elephant use. The use of degraded forests has important implications for the protection of forests that may otherwise have a high chance of land use change. We sought to build on this concept and identify areas of intact forest that were important ADCs between these highly suitable zones and classify their habitat features. HSLT movement analysis suggests that ADC areas do exist throughout the range, and when these are examined in a stepwise movement manner, topological features are found to be the most important factor driving elephant movement. In line with previous studies of African and Asian elephants (Storer, 1981; Vanleeuw & Gautier-Hion 1998), movement in directions of increased relative elevation are likely indicative of elephants following ridgelines when moving quickly through landscapes. There was evidence of potential ridgeline utilization in both corridors utilized for SSF analyses and those without sufficient connective data strings for pathway analysis. This finding, coupled with potentially decreasing TCH levels at increased elevation, corroborates the indication that ridgelines could potentially provide important corridor habitat.

Oil palm plantations appear to play a role, not just in elephant feeding, but also in facilitating movement between forest habitats (Skara et al. unpublished data). A total of 27% of HSLT trajectory movements were found to occur in large-scale agricultural plantations. Elephants therefore continue to utilize agricultural lands, and exhibit corridor-like behavioral patterns within these landscapes, with this partly contributing to the 24% lower overall ACD at HSLT locations. Low ACD values generally indicate degraded and fragmented landscapes, and due to the relative abundance of a variety of grass species present in plantations, these areas could provide large-scale feeding opportunities for elephants (English et al. 2014a, 2014b; Yamamoto-Ebina et al., 2016). Increases in HSLT movements could relate to flight responses or movements to avoid interactions with humans, with elephant patrols and oil palm workers becoming incidental poachers, as well as the potential for increases in elephant interactions with domestic animals. Whilst flight responses could be attributed to some of these HSLT incidences, shortcuts to adjacent forests and access to feeding grounds are also a likely cause of at least some of these behaviors, as evident in a number of the defined ADCs (Fig. 4). Despite an abundance of small-scale agriculture in the vicinity of urban centers, the presence of elephants in these areas was low, suggesting that elephants actively avoid conflict with people, and related activities.

Due to the restricted habitat exhibited in the LKWS population, the thresholds for HSLT movements utilized here were met too often to enable effective corridor delineation. This suggests a very different behavioral strategies occurring in these highly restricted landscapes and could point to the fact that plantations, as a source of food, actually enable higher densities of elephants in the LKWS compared to other populations. It is also possible that this area has historically high densities, owing to the increased presence of clay and salt licks, as well as natural grasslands. Indeed, the fact that over a quarter of HSLT trajectory movements occur within plantations suggests that ADC behavior, as a total proportion of behaviors in a given habitat, is occurring on a more frequent basis here than in natural habitats. This is likely due to a combination of factors: firstly, mature oil palm provides little in the way of food for elephants (Oliver, 1978), although palm oil kernels and the shoots of newly-planted palms are sometimes eaten (Susanto and Ardiansyah, 2003; Suba et al., 2018). Selection of newly replanted areas might explain a number of the HSLT movements, as elephants move rapidly through mature oil palm plantations in search of areas with young palms or areas of recent palm felling where chipped palms provide feeding opportunities. However, oil palm plantations can also be an abundant source of grass, which is a large component of elephant diet, especially in less mature plantations where less shading is created by an absence of mature palms (English et al., 2014a). Secondly, conflict avoidance in edge habitats is likely to illicit HSLT behaviors because elephants move through these areas as quickly as possible. Finally, anti-elephant activity in plantations (e.g. the use of cannons and shotguns, burning of tires, and regular patrolling) could result in flight behavior in these areas. The fact that so many of the repeat-use ADCs occur in edge or plantation habitats suggests that these are chronic issues rather than isolated incidences or responses.

Urbanization of once remote landscapes, as is rapidly occurring across Sabah (McMorrow and Talip, 2001) and is a growing problem throughout tropical regions, is impacting wildlife movement, transmission of disease and biodiversity (Bradley and Altizer, 2007; Ditchkoff et al., 2006). Such urbanization is often the source of increasing levels of human-wildlife conflict (Soulsbury and White, 2016). Only 1.54% of elephant GPS locations, and just 0.26% of HSLT movements, occurred within a 1 km buffer of urban areas, including villages and roads, suggesting active avoidance of urbanized areas by elephants despite increasing levels of human-elephant conflict throughout Sabah. Whilst this broad-scale finding supports avoidance of urbanization, other studies have demonstrated that roads are locally attractive to Asian elephants in Peninsular Malaysia and provide enhanced feeding opportunities (Wadey et al., 2018). It has, however, also been shown that roads actively increase poaching prevalence (Laurance et al., 2006; Trombulak and Frissell, 2000), providing impetus for avoidance by elephants. Our data on active avoidance of urban areas suggests that increases in Bornean elephant mortality are not adequately explained without significant increases in incidences of active hunting and ivory poaching. Sabah has experienced increasing levels of poaching, with many examples including tusk removal, with a number of high-profile criminal investigations (New Straits Times, 2019a,b; The Borneo Post, 2019), and suggestions that dowries are one of the primary drivers (New Straits Times, 2019a,b).

Our study provided a detailed investigation of both fine- and landscape-scale ranging of endangered Bornean elephants, providing a more detailed understanding of elephant habitat utilization. However, there remain a number of questions for future work to explore. Firstly, a more detailed understanding of aspects of oil palm habitat use and feeding regimes by elephants would provide a clearer indication of their use, in terms of useable habitat versus merely for travel between habitat patches (or, alternatively, how areas utilized for feeding or travel can also result in disturbance-initiated flight responses). Secondly, a more detailed analysis of ridgelines within the CS forest block would provide priority areas for protection to enable connectivity between habitat blocks. The identification of ADCs throughout the landscape provides both local indications of areas important for elephant movement, as well as a more generalized conservation planning consideration regarding the protection of forests in the future. From a management perspective, these ADCs can be used to identify habitat linkage within populations, as well as to suggest how it may, in the future, be feasible to reconnect geographically isolated populations. Finally, having shown the scale of elephant use of agriculturally dominated landscapes, a broad-scale human-elephant conflict assessment is urgently needed, including an evidence-based prioritization of anti-poaching measures intended to quell the marked increase in poaching that is occurring within these once isolated elephant populations.

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Appendix A. Supplementary data

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